

A REVISION OF THE NORTH AMERICAN SPECIES OF HELIANTHEMUM (CISTACEAE)

H. S. DAOUD AND ROBERT L. WILBUR*

The genus *Helianthemum* s.l. is composed of approximately one hundred species found in both the New and the Old World. The species are particularly abundant about the Mediterranean Sea and in North America. The American species, as well as those of the rest of the world, were most recently revised in their entirety by Grosser (Engler's Pflanzenreich 14. (IV. 193.) 1903). Several regional treatments for the North American species have been since published but no comprehensive account of the genus in North America has appeared. Since Grosser's monograph, several additional American species have been proposed.

The generic dismemberment of *Helianthemum* has continued to be a source of considerable disagreement. This study, however, was not intended to evaluate the generic relationship of the American species with those of the Old World but to review the North American representatives. The troublesome question of generic limits deserves careful reappraisal but ought to be undertaken where collections of the entire generic complex are readily available. Twenty North American species of *Helianthemum* are recognized in this account.

Our geographical area 'North America' includes the West Indies and Central America. This treatment therefore includes all the species in the New World except the three known from South America. These were excluded primarily because too little material was readily available to make their study feasible. One species, *H. brasiliense* (Lam.) Pers., is known from the eastern side of that continent,

*The present study is based largely on the dissertation which the senior author presented to the Graduate School of Duke University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Duke University. The junior author's role in this investigation was made possible by NSF Grant 18799 for which grateful acknowledgment is made.

occurring in Brazil, Uruguay and Argentina, while two others, *H. hirsutissimum* Presl and *H. spartioides* Presl, are found in Chile. The last mentioned species is of particular interest since its relationship is reported to be with the Californian *H. scoparium* Nutt.

HISTORY OF THE GENUS IN NORTH AMERICA

Although the names *Helianthemum* and *Cistus* were in use earlier, Tournefort (Inst. Rei Herb. 1700.) recognized two genera on the basis of their capsule differences: *Helianthemum* having but one locule and *Cistus* with 5 (6-10) locules.

Linnaeus (Sp. Pl. 523-529. 1753 and Gen. Pl. 234. 1754.) did not accept Tournefort's *Helianthemum*. Instead he combined it with *Cistus*, which he placed in the first order (Monogynia) of his thirteenth class (Polyandria). He recognized 28 species of *Cistus* including one New World species, *Cistus canadensis*. Two years earlier, Linnaeus described *Lechea major* which he later included in Species Plantarum in the class and order Triandria Monogynia. Blake (Rhodora 20: 49-50. 1918), found the type of *Lechea major* to be conspecific with *Cistus canadensis*.

Nomenclaturally, the genus is attributed to Miller (Gard. Dict. Arb. 1754.), whose Fourth Edition, although pre-Linnean in character, is still an acceptable source of generic names.

Rafinesque (Car. Nuov. Gen. Sp. Sicil. 73. 1810.) proposed the generic name *Xolantha* to replace *Helianthemum* since the latter could be confused with *Helianthus* (Compositae). Later Rafinesque (Chlor. Aetn. 9. 1815.) proposed the generic name *Anthelis* as another substitute for *Helianthemum*.

Dunal (DC. Prodr. 1: 266-284. 1824.) recognized 112 species of *Helianthemum* and divided the genus into three "series" and nine sections primarily on the bases of differences of stigma, style and stamens.

Dunal's section *Lecheoides* contained only the seven species of *Helianthemum* adequately known to him from the New World (*H. corymbosum*, *H. rosmarinifolium*, *H.*

glomeratum, *H. ramuliflorum*, *H. canadense*, *H. brasiliense*, and *H. carolinianum*). It would seem that the American occurrence of these species and their alternate cauline leaves were their principal claim to separate sectional ranking.

Sweet (Cistineae. 1825-30.) adopted Dunal's classification and listed four more species with the seven American species which Dunal had assigned to his section *Lecheoides*. Three of these (*H. obcordatum*, *H. tripetalum* and *H. astylum*) Dunal previously had listed as unsatisfactorily known to him and they were known no better by Sweet. The fourth species, *H. polygalaeifolium* Sweet, is generally considered a synonym of *H. brasiliense*. Sweet indicated that several New World species produced petaliferous flowers in the summer and apetalous flowers in the autumn, a feature he expected was characteristic of all American species.

Spach (Ann. Sci. Nat. 2nd ser. 6: 357-375. 1836.) recognized sixteen genera in the Cistaceae. The known species of *Helianthemum s.l.* were placed in eight of these genera. Five of these eight genera were restricted to the Old World. The other three, *Crocanthemum*, *Heteromeris* and *Taeniostema*, all newly described, occurred only in the New World. The primary points in Spach's account of the New World genera are as follows:

Crocanthemum: flowers all petaliferous. (*C. carolinianum* (Walt.) Spach and *C. brasiliense* (Lam.) Spach were both definitely included and *Helianthemum polygalaeifolium* Sweet was indicated as a possible addition.)

Heteromeris: both petaliferous and apetalous flowers present. (Included in this genus were taxa which are today known as *Helianthemum glomeratum*, *H. canadense*, *H. corymbosum* and *H. rosmarinifolium* but which were in several cases provided by Spach with new epithets under *Heteromeris*.)

Taeniostema: flowers all apetalous. (The only species included was *T. micranthum* to which he appended *Helianthemum glomeratum* as a questionable synonym.)

A fundamental weakness of his last two genera was the

inclusion of different floral states of *H. glomeratum* within both taxa. Most American authors who accept generic status for the American species have taken up the generic name *Crocanthemum*. Although this genus was originally characterized by the constant petaliferous condition of its flowers, a feature not strictly true of either of the species originally included and certainly correct for only a minority of the species included by those who have accepted the genus, this in itself would not bar the employment of the name for the American segregate.

The subgenus *Horanthes* was proposed by Rafinesque (New Fl. N. Am. 3: 30 + 31. 1838.) as a substitute for Dunal's section *Lecheoides* since, in his opinion, the latter too closely resembled the generic name *Lechea*. Later in the same year he elevated (Sylva Tell. 132 + 133. 1838.) *Horanthes* to generic status along with four other segregates from the Old World: *Stegitris*, *Fumana*, *Xolanthes* (= *Xolantha*), and *Psistina*.

Willkomm (Icon. et Descr. Pl. 2: 8-12. 1856.) proposed a new classification for Cistaceae dividing it into eleven genera. He accepted Spach's genera, *Crocanthemum*, *Heteromeris* and *Taeniostema*, to which both workers had assigned all the known New World species. *Crocanthemum* and five Old World genera comprised his Tribe Normales possessing only chasmogamous flowers while *Heteromeris* and *Taeniostemma* (= *Taeniostema*) were placed in his Tribe Abnormes since they possessed cleistogamous flowers.

Bentham (Gen. Pl. 1: 113 + 114. 1862.) maintained the genus in the broader sense, indicating that the characters used in separating the species of *Helianthemum* into supposed genera by Spach and others were minor and inconstant.

The Synoptical Flora (Gray's Syn. Fl. 1(1): 189-191. 1895.) accepted nine species of *Helianthemum* in the United States which were arranged in three groups. The first group contained the "Atlantic species, with dimorphous flowers" (*H. canadense*, *H. majus* (= *H. Bicknellii*), *H. capitatum* (= *H. rosmarinifolium*), and *H. corymbosum*). The second included the "S. Atlantic species with homomor-

phous flowers" (*H. arenicola*, *H. Nashii*, and *H. carolinianum*). Barnhart (Bull. Torrey Club 27: 589-592. 1900.) pointed out that *H. arenicola* and *H. Nashii* were apparently placed among the species with homomorphous flowers on the basis of their original description since both possess cleistogamous as well as petaliferous flowers. Gray's third group consisted of the "Pacific species: flowers homomorphous" (*H. scoparium* and *H. Greenei*).

Reiche (Nat. Pflanzenfam. III. 6: 304-306. 1895.), employing *Helianthemum* in the broad sense, treated all of Dunal's sections as subgenera except *Macularia* which was omitted. All the New World species were placed in the subgenus *Lecheoides* (Dunal) Reiche.

Grosser (Pflanzenreich 14 (IV. 193.) 1-161. 1903.) assigned all known species of *Helianthemum* s.l. to three genera: *Halimium*, *Tuberaria*, and *Helianthemum*. *Tuberaria* and *Helianthemum*, both confined to the Old World, supposedly resemble one another in possessing either no style or one that is bent or curved and often elongate as well, somewhat swollen funiculi and only petaliferous (chasmogamous) flowers. *Halimium* (Dun.) Wilk., found according to Grosser's concept both in the Old and New World, was reported to differ from them in its short, straight style, filiform funiculi and often apetalous (cleistogamous) flowers in addition to the petaliferous. There were also differences reported for the embryos of the three genera.

Grosser recognized three sections in *Halimium*. Section *Spartioides*, containing the Californian endemics, *H. scoparium* and *H. occidentale* (= *Helianthemum Greenei*), and the Chilean *H. spartioides*, was characterized primarily by its supposed broom-like habit. The Old World section *Eupalimium* was distinguished principally by possessing only chasmogamous flowers while the American section *Lecheoides* often has cleistogamous as well as chasmogamous flowers.

Britton (Ill. Fl. N. U.S. 2: 539-541. 1913.) transferred the three species of *Helianthemum* then recognized within the range of the Illustrated Flora to Spach's *Crocanthemum*. In the same year Bicknell (Bull. Torrey Club 40: 613-616.

1913.) accepted this generic segregate. However, Fernald (*Rhodora* 19: 58-60. 1917.) rejected the idea of separating the New World species into the endemic, segregate genus *Crocanthemum*.

Ponzo (*Nuovo Gior. Bot. Ital.* 28: 157-173. 1921.) basing his classification on anatomical and morphological features, included the seven New World species known to him in Spach's genus *Heteromeris*.

Standley (*Contr. U.S. Nat. Herb.* 23: 832-834. 1923.), following Grosser, treated all nine Mexican species of *Helianthemum* known to him in the genus *Halimium*.

Janchen (*Österr. Bot. Zeitschr.* 71: 266-270. 1922.) followed Britton and Bicknell in accepting the segregation of the New World species in Spach's genus *Crocanthemum*. He indicated that these species have alternate, pinnately nerved leaves while the Old World species of *Halimium* have opposite, three nerved leaves. Janchen (*Engler & Prantl's Nat. Pflanzenfam.* 2 Aufl. 21: 289-313. 1925.) included all the species of *Helianthemum* (*sensu lat.*) in four genera: the New World *Crocanthemum* and three genera from the Old World. The species of *Crocanthemum* were aligned in two sections, *Spartioides* and *Lecheoides*, which were previously recognized by Grosser (*Engler & Prantl's Nat. Pflanzenfam.* 14. IV. 193. 33. 1903.) as sections of *Halimium*.

Barnhart (in *Small's Man. Se. Fl.* 878-880. 1933.) followed Britton, Bicknell, and Janchen in accepting *Crocanthemum*. He also arranged the nine species genus into three informally designated groups.

Schreiber (*Madrono* 5: 81-85. 1939.) studied the genus *Helianthemum* in California, accepting the two previously recognized species and three varieties, and proposed a new species, *H. suffrutescens*.

Fernald (*Rhodora* 43: 609-616. 1941.) for the second time questioned the status of the segregate genus *Crocanthemum* and the way it was applied to the species of the New World. He indicated that the characteristics proposed by various authors as a basis for the segregation of the New World species into a single genus were inconstant.

MORPHOLOGY

The HABIT of all American species is perennial. The genus contains herbaceous, suffruticose and fruticose growth forms. The ten species found in the eastern half of the United States, Canada, and the West Indies are typically herbaceous while the two Californian species are suffruticose. The Baja Californian species, *H. nutans*, is definitely shrubby although low and divergent. Three Mexican and Central American species (*H. Pringlei*, *H. Coulteri* and *H. patens*) may be either herbaceous or suffruticose, while the remaining Mexican and Central American species are all suffruticose. The habit of the species is of minimal value in identification.

PUBESCENCE varies greatly in both quality and quantity on different parts of the plant. All the American species are typically pubescent although occasional specimens of *H. patens* are completely glabrous. The basic types of pubescence found among the North American species are (1) stellate hairs, the predominant type varying greatly in both length and density; (2) simple hairs, longer than the stellate hairs but less abundant and usually intermixed with them; (3) glandular hairs, very rare but typically found on the calyces of *H. dumosum* and always on the inflorescence as well as the upper part of the stem in *H. Greenei* and occasionally on the calyces of *H. carolinianum*, *H. Coulteri* and *H. canadense*. They are conspicuous only in *H. Greenei*.

Aside from habit and pubescence, few features of the STEM are taxonomically useful. Usually the stem is pubescent although in some species it is glabrate, or in a few specimens of *H. patens* completely glabrous. Among the species of the southeastern United States, *H. carolinianum* alone has stems sparsely covered with elongate, hyaline stellate pubescence. Among the Mexican species, the stems of *H. chihuahuense* and sometimes those of *H. Pringlei* are villous. *Helianthemum propinquum* characteristically arises from a creeping subterranean rootstock, and this distinguishes it from the closely related *H. Bicknellii* which like most American species possesses a woody caudex.

The LEAVES are simple, pinnately but often obscurely

veined, estipulate, and alternate. STIPULES have been reported in certain species (e.g. *Crocanthemum stipulatum* Janch.) but these are the result of a mistaken interpretation of fasciculate axillary leaves. A few species possess basal leaves in rosettes or crowded at the base of the plant but these differ in no essential way from the lower cauline leaves. These have been reported as opposite but actually are alternate and separated by very short internodes. The presence of basal leaves is often characteristic of *H. carolinianum* and *H. georgianum*. Occasionally, however, *H. rosmarinifolium* or a few other species also have basal leaves.

PETIOLES are present in a majority of the species. A few species may be either epetiolate or with a petiole up to 3 mm. long. Sometimes no definite distinction can be made between the blade and petiole. This renders the presence or absence of the petiole of negligible taxonomic value.

The shape of the BLADES varies from linear to broadly obovate. Although the shape is characteristic for some species, it varies greatly in others. Also there is the expected gradual decrease in size and change in shape of the lamina from the base of the plant upward. The shape of the leaf-blade, therefore, is of limited aid in distinguishing the species and has been employed only as a supplementary character.

The PUBESCENCE of the leaves is essentially of two types: (1) the predominant stellate hairs which vary greatly in both length and quantity, and (2) the relatively uncommon simple hairs which are longer, less abundant and usually intermixed with the stellate type. (Simple foliar trichomes occur on the upper leaf surface of *H. canadense*, *H. dumosum*, and sometimes *H. Coulteri*, both surfaces of *H. chihuahuense* and sometimes also on *H. Pringlei*, and only on the leaf margin of *H. nutans*). The leaves of all species examined are typically pubescent, but those of *H. scoparium* and *H. Greenei* sometimes are glabrate and occasionally those of *H. patens* are completely glabrous.

The pubescence on both surfaces of the leaves is similar in quantity and quality in some species (*H. Greenei*, *H. scoparium*, *H. Pringlei*, *H. chihuahuense*, *H. patens*, *H.*

argenteum, and *H. nutans*) and in these species the secondary veins are not elevated below. In other species (*H. canadense*, *H. dumosum*, *H. Bicknellii*, *H. propinquum*, *H. carolinianum*, *H. rosmarinifolium*, *H. georgianum*, *H. corymbosum*, *H. concolor*, and usually *H. Coulteri*) the quality and the quantity of the pubescence are remarkably dissimilar on both surfaces of the leaves, and in these the secondary veins are prominently elevated beneath. Both leaf surfaces of *H. glomeratum* possess similar pubescence but its venation varies from obscure to prominent. *Helianthemum arenicola* has obscure secondary veins on the lower surface of the leaf but the pubescence differs somewhat (largely in color) on the two sides. The secondary veins of *H. Nashii* vary from obscure to prominent, and the pubescence differs on the two surfaces.

Among the species with prominent secondary venation beneath only *H. carolinianum* and *H. concolor* have leaves sparsely stellate-pubescent while the remaining prominently veined species are so densely stellate-tomentose that the lower surfaces of their leaves are not visible.

In spite of the indicated variability, the pubescence and the secondary veins are taxonomically helpful in distinguishing the species.

The MARGINS of the leaves of *H. carolinianum* are sub-denticulate while those of the remainder of the species are entire. The margins of some species are characteristically revolute.

The INFLORESCENCES of the American species are remarkably diverse as to type, position, and structure. It may consist of: (1) all chasmogamous flowers varying from solitary (as in *H. canadense*) to numerous (as in *H. Greenei*); (2) many chasmogamous flowers and few cleistogamous ones as in *H. Coulteri*; (3) few chasmogamous flowers and many cleistogamous ones as in *H. corymbosum*; and (4) all cleistogamous flowers, varying from a solitary flower as in *H. argenteum* to numerous as in *H. glomeratum*.

A few species (*H. scoparium*, *H. Pringlei*, *H. Coulteri*) have unusually variable inflorescences. Other species (*H. canadense*, *H. dumosum*, *H. Bicknellii*, *H. propinquum*, and to a much lesser extent *H. chihuahuense*) have two types of

inflorescence which mature at different times in the growing season and in different positions on the plant, resulting in great variability in aspect. However, the inflorescence is characteristic for most species and hence has proved to be a useful diagnostic feature.

The BRACTS of *H. corymbosum* are obtusely spatulate-linear while those of the remaining species are acutely linear or lanceolate.

The PEDICELS of the chasmogamous flowers range from shorter than to about five times longer than the calyx. As a taxonomic character, the pedicel has been greatly over-emphasized and its variability minimized. The cleistogamous flowers may be sessile or pedicellate.

The FLOWERS are either chasmogamous (pollination apparently effected after expansion of the floral envelope) or cleistogamous (with pollination occurring within the closed perianth). When these two kinds of flowers are borne on the same plant, the CHASMOGAMOUS flowers are earlier and usually longer pedicellate. They are characterized also by a larger calyx, five fugacious petals, more numerous stamens (10 or more), and by larger fruits which usually contain more numerous seeds. Their anthers are usually longer than wide and dehisce along their entire length. The CLEISTOGAMOUS flowers lack petals and are borne later (but may fruit earlier) and possess shorter pedicels, a smaller calyx, and fewer stamens (3-8). The anthers of the cleistogamous flowers are as long as wide or shorter and dehisce only by a break in the wall adjacent to the stigma to which they adhere.

Four species (*H. Greenei*, *H. scoparium*, *H. nutans*, and *H. patens*) possess only petaliferous flowers. Cleistogamous flowers are very rare in *H. carolinianum*, while all of the remaining species are dimorphic, possessing both chasmogamous and cleistogamous flowers. The Mexican *H. glomeratum* is the only species in which some of its members apparently produce only cleistogamous flowers.

The CALYX is composed of five sepals in two dissimilar series: two narrower and usually shorter outer sepals and three inner sepals. The inner three constitute the prominent calyx. The outer and the inner sepals are united near the

base in some species (e.g. *H. Bicknellii*, *H. scoparium*), while in others the fusion extends half or two thirds of their length (e.g. *H. propinquum* and *H. Coulteri*).

The calyces are characteristically pubescent in all species, although they are sometimes glabrate in *H. scoparium*, or occasionally even completely glabrous in *H. patens*. The calyces of some species are covered with stellate pubescence of varying quality and density, while the calycine stellate pubescence of other species is intermixed with simple hairs and/or glandular hairs.

The CHASMOGAMOUS OUTER SEPALS are variable in shape, length, and degree of fusion with the inner ones. They are useful in distinguishing species especially when combined with other characteristics. The southeastern *H. corymbosum* alone has spatulate outer sepals with the apices obtuse or nearly so, while the other species have linear or lanceolate sepals with acute apices. The amount of the fusion between the inner and the outer sepals and the length of the free portion of the outer ones are of significance in distinguishing the closely related *H. Bicknellii* and *H. propinquum*.

The CHASMOGAMOUS INNER SEPALS are typically ovate or ovate-lanceolate with acute to acuminate apices except in *H. Nashii* whose inner sepals are asymmetrically oblique. The length of the inner sepals is exceedingly variable even within the same species and hence offers no serviceable diagnostic character.

The CLEISTOGAMOUS OUTER SEPALS are mostly linear and attached near the base of the inner ones. In contrast the free portion of the outer sepals of *H. canadense* and *H. propinquum* is a rudimentary knob about twice as long as wide and fused to the middle edge of the inner sepals.

The CLEISTOGAMOUS INNER SEPALS vary but little, being either ovate or ovate-lanceolate, with acute to acuminate apices. Two unrelated species, *H. Nashii* and *H. canadense*, are unusual in possessing sepals asymmetrically oblique at their apices. In most of the species the cleistogamous flowers are so small that most measurements were made at the fruiting stage.

The COROLLA is present in the chasmogamous flowers and is fugacious. Cleistogamous flowers lack petals. The petals

are essentially yellow but those of *H. Pringlei* are sometimes tipped or margined with purple. The shape of the petals is more or less uniform among the species and usually longer than the calyx at anthesis. The variation in petal size within a species is great. For example, the range is between 2.4-5.0 mm. long in *H. patens*, and 8-16 mm. long in *H. carolinianum*.

ANTHER-DEHISCENCE is one of the best ways to distinguish chasmogamous from cleistogamous flowers. This is especially true in fruiting specimens when the petals and some of the stamens have fallen which alone in the past have been relied upon to distinguish the two types of flowers. In the chasmogamous flowers stamen-number varies between 10-50. The small-flowered species, such as *H. argenteum*, have 10-15 stamens, while the larger-flowered species, like *H. carolinianum*, have 20-50. The length of the filament as well as that of the anthers is quite variable. The anthers of the chasmogamous stamens, which neither cohere to each other nor adhere to the stigma at anthesis, are oblong to linear, (1-) 1.5-2 times longer than wide and dehisce throughout their entire length. In the cleistogamous flowers, the number of the stamens is also variable (3-8). Their anthers are coherent to one another and adherent to the stigma at anthesis and even in fruit for most species. These anthers dehisce by the rupture of their walls adherent to the stigma.

There is such great variation in the size of the PISTIL and its parts that their size is of no taxonomic use. However the stellate-pubescent ovaries of *H. Nashii* and *H. arenicola* are most helpful in distinguishing them from all other species.

The chasmogamous pistils are larger than the cleistogamous ones in the same species. The ovaries of the chasmogamous flowers are ovoid or nearly so and unilocular with few to many ovules. The styles of these flowers vary in length from wanting or nearly so in *H. Coulteri* to nearly as long as the ovary in *H. glomeratum* but never exceeding 1 mm. in length. The styles of the chasmogamous flowers, when present, are always erect and straight in American species and their stigmas are capitate and vary greatly in diameter.

The cleistogamous pistils are so small that they usually have not been measured. However, their ovaries are ovoid and similar to the chasmogamous pistils of the same species in carpel-number and pubescence. Their styles are very short and are much exceeded in height by the ovaries of the same flower.

The CAPSULES of both chasmogamous and cleistogamous flowers are loculicidally dehiscent. Previously the capsules of all species of *Helianthemum* were thought to be 3-valved. However *H. Nashii* characteristically is 2-valved. Only two species, *H. Nashii* and *H. arenicola*, possess stellate-pubescent capsules while those of the other American species are glabrous.

The variation in size and shape of the chasmogamous capsules is so great as to be taxonomically useless. The capsules are shorter than the calyx (or rarely slightly longer in *H. Pringlei*). The chasmogamous capsules typically persist throughout the growing season, but in both *H. Bicknellii* and *H. propinquum* they usually fall immediately after maturation.

The largest capsules, often containing more than one hundred seeds, are found in *H. carolinianum* and the smallest capsules, with only 1-3 (-6) seeds, occur in *H. rosmarinifolium*. Chasmogamous capsules are apparently produced by all species, although many specimens bear only cleistogamous capsules.

The cleistogamous capsules vary in shape and size but are always shorter than the calyx. The largest cleistogamous capsules, containing up to 22 seeds are borne by *H. Coulteri* and the smallest capsules, with only one or rarely two seeds, are found in *H. rosmarinifolium*. Four species of course lack cleistogamous capsules. No cleistogamous capsules were seen in *H. carolinianum*, which is not surprising since less than one per cent of the specimens studied had cleistogamous flowers. The number of the cleistogamous seeds per capsule is reasonably constant and hence helpful in identification.

Except for the number and size, the SEEDS produced by both chasmogamous and cleistogamous fruits in the same species are similar.

The seeds of twelve of the species studied are covered with a thin membrane, which is separable after the seeds are moistened with water for a few seconds. Such a membrane is usually yellowish or sometimes spotted with brown, but in *H. nutans* and *H. argenteum* white papillae occur.

The seeds of the remaining species (*H. canadense*, *H. dumosum*, *H. carolinianum*, *H. Coulteri*, *H. Bicknellii*, *H. propinquum*, *H. Nashii* and *H. arenicola*) do not have a readily separable membrane. The seeds of *H. canadense*, *H. dumosum*, and *H. carolinianum* are papillate. The seeds of *H. Coulteri* are mostly papillate but in plants from Central America are often reticulate. Those of *H. Bicknellii* and *H. propinquum* are usually reticulate, while the seeds of *H. Nashii* and *H. arenicola* are pebbled to papillate. The sculpturing of the seed coats often provides useful diagnostic features.

The seeds of most of the species have a somewhat transparent endosperm especially if examined when moist and after removal of the membrane. The embryos are curved, possess linear cotyledons, and are enveloped by the endosperm. They can easily be excised by rupturing soaked seeds.

EVOLUTIONARY RELATIONSHIPS

The American species of *Helianthemum* show numerous morphological trends which probably are best interpreted as evolutionary tendencies. Speculation as to evolution is of necessity highly subjective when facts are few but still it would seem desirable to record our feelings as to relationships. We are aware of the shortcomings of such a proposed "phylogenetic tree" as is presented in figure 1, but offer it in hopes that it will stimulate other investigations in this genus and thereby supplement the all too scanty morphological data. The more obvious evolutionary tendencies are thought to be the development of cleistogamous flowers, the appearance of a hygroscopic testa and changes in inflorescence-type. There also seem to be established trends for decrease both in the size of floral parts and fruit accompanied by reduction in the number of seeds per capsule. In one species the carpel number has been reduced to two.

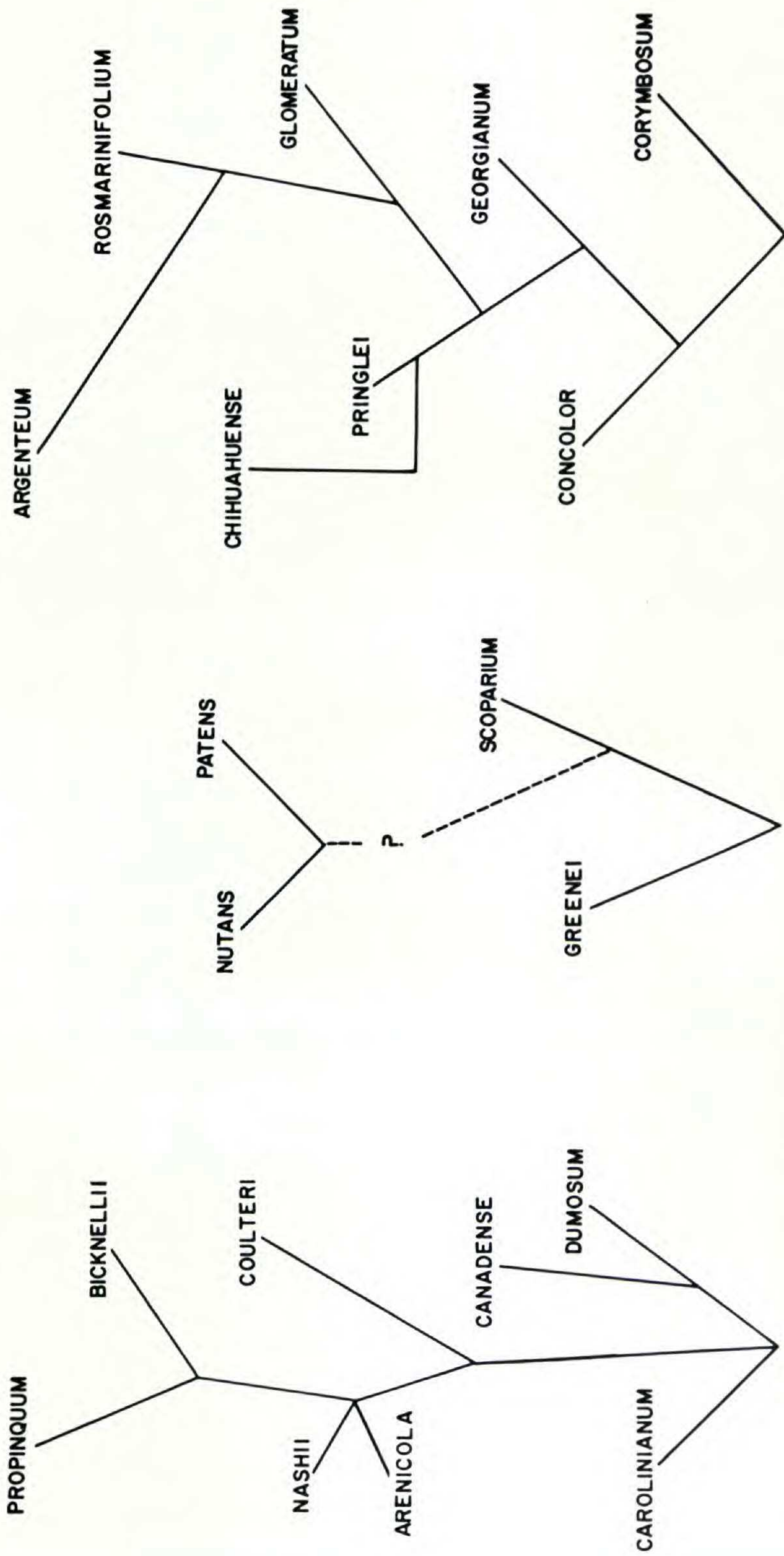


Fig. 1. Possible relationship of the North American species of *Helianthemum*.

The supposedly more primitive species are presumed to possess only petaliferous, chasmogamous flowers. The presence of cleistogamous flowers is therefore considered an evolutionary advance. The four species lacking cleistogamous flowers are quite diverse and perhaps not closely related. There is no evidence that they are derived from taxa that once had cleistogamous flowers. Although possessing only chasmogamous flowers, it is felt that they still are evolutionarily more advanced than members (e.g. *H. canadense* and *H. dumosum*) that have cleistogamous flowers. The presence of a hygroscopic testa in these species would suggest a possible relationship with the supposed more advanced alliance. It is of course generally accepted that evolutionary progression does not proceed uniformly in all structures of any given taxon.

Three principal evolutionary lines perhaps exist within the North American species. The four species which lack cleistogamous flowers possibly represent one line but their great diversity might be an indication that they are an unnatural assemblage of primitive species. Among the species which develop cleistogamous flowers two lines are apparent. The supposedly most advanced of the three lines consists of those species with a hygroscopic seed coat. The members of the presumed most primitive alliance have seeds lacking this hygroscopic testa. It has not appeared wise to recognize formally the three suggested evolutionary lines as taxonomic series or sections since each is characterized by only one feature. It is felt that formally designated taxa ought to have more than one feature indicating their common origin. Since the arrangement presented here is admittedly tentative, there seems to be no urgency in formal designations.

Eight species were recognized in the more primitive line characterized by papillate, pebbled or reticulate seeds lacking the hygroscopic seed coat. *Helianthemum carolinianum* is considered the most primitive American species for the following reasons: (1) the rarity of cleistogamous flowers; (2) the most primitive type of inflorescence (a scorpioid cyme) in this line; (3) the largest capsule which produces the greatest number of seeds; (4) the most numerous

stamens. Barnhart (Bull. Torrey Club 27: 592. 1900.) has, however, indicated that this taxon seems to him "like a heteromorphous species which has lost its apetalous form of flowers" and he suspected that "if its origins could be traced, to find it had heteromorphous ancestors."

Both *H. dumosum* and *H. canadense* are apparently very closely related and have been even treated as one species until this century. The chasmogamous calyces of these two species approach those of *H. carolinianum* in size. *Helianthemum dumosum* is here considered more primitive than *H. canadense* since it possesses both fewer and larger cleistogamous capsules containing more numerous seeds. Its chasmogamous flowers are usually larger than those of *H. canadense*. In addition the cleistogamous outer sepals of *H. canadense* are more reduced, being almost rudimentary. Also there is no sharp differentiation between the late chasmogamous flowers and the cleistogamous ones in *H. dumosum*. The fact that the range of *H. dumosum* is very restricted and confined entirely to a glaciated region in contrast to the widespread *H. canadense*, however, might argue for another interpretation.

The unusually variable *H. Coulteri* often possesses a chasmogamous calyx nearly as large as those of *H. canadense* and *H. dumosum*. Its relationship to those two species is perhaps indicated by the frequent intermixture of stellate pubescence and pilose hairs on the chasmogamous calyx. Also the leaves sometimes resemble those two northern species in having the upper surface both stellate-pubescent and pilose. *Helianthemum Coulteri* is judged as more advanced than either *H. canadense* or *H. dumosum*, in spite of its fewer but larger cleistogamous flowers.

The southeastern *H. arenicola* and *H. Nashii* are unique among the American species in possessing stellate-pubescent ovaries and capsules. Of the two, *H. arenicola* is considered the more primitive since it has larger chasmogamous flowers, more seeds in each cleistogamous capsule and the characteristic 3-valved capsule rather than two which *H. Nashii* alone possesses in the genus. It is suggested that these two species are more advanced than the preceding members of this line because they have smaller chasmoga-

mous flowers and fruit and fewer seeds/chasmogamous capsule. Also their outer sepals are narrower and shorter than the earlier-mentioned and supposedly more primitive species.

The two closely related species, *H. Bicknellii* and *H. propinquum*, are perhaps more advanced than the other rough-seeded species since their numerous cleistogamous capsules are smaller and contain fewer seeds. *Helianthemum propinquum* is possibly more advanced than *H. Bicknellii* since it has fewer chasmogamous flowers and a much smaller free portion of the outer sepals. *Helianthemum propinquum* has smaller cleistogamous outer sepals and generally smaller cleistogamous capsules. Although *H. propinquum* is ranked as the most advanced species in this evolutionary line, it is thought to be more primitive than some members of the other supposed phylads.

The four Mexican and Californian species lacking cleistogamous flowers (*H. Greenei*, *H. scoparium*, *H. nutans* and *H. patens*) perhaps represent an independent line but are so dissimilar that placing them together may be unwarranted. Among them *H. Greenei*, a narrow endemic to the Channel Islands of California, is treated as the most primitive because of its broader, lanceolate outer sepals. The more widespread and variable *H. scoparium* is related to *H. Greenei* but has narrow, linear, outer sepals. The remaining strictly chasmogamous species, *H. nutans* and *H. patens*, possess a different habit and are believed to be more advanced, as indicated by reduction in number of flowers and size of leaf. By similar reasoning *H. patens* would be considered more advanced than *H. nutans* since its flowers are smaller with fewer stamens and fewer seeds/capsule. In addition the herbaceous habit of *H. patens* contrasted with the fruticose habit of *H. nutans* might be considered as an evolutionary advance. These four species possess a hygroscopic testa which also characterizes the supposedly more advanced evolutionary line with cleistogamous flowers.

The most primitive member of the line with a hygroscopic seed-coat is possibly *H. corymbosum*. Its more foliaceous outer sepals and bracts may indicate its relative primitiveness. It also is the only species in this line possessing the

prominent and persistent funiculi and placentae which are found also in the three supposedly more primitive species of the non-hygroscopic seeded alliance. It is suggested that *H. concolor* is another primitive species. It possesses the largest leaves and the longest outer sepals of any member of the hygroscopic-seeded alliance. It is treated here as more advanced than *H. corymbosum* because of its much narrower outer sepals and bracts and fewer seeds in each of the cleistogamous capsules.

The next more advanced species within this line are perhaps *H. georgianum* and *H. Pringlei*. These two species have a supposedly reduced and hence more advanced inflorescence-type (a racemose cyme), and their outer sepals are reduced in size. *Helianthemum georgianum* may be more primitive than *H. Pringlei* as it has more numerous seeds in its cleistogamous capsule.

It is felt that *H. chihuahuense* is more advanced than the two preceding species since its chasmogamous and cleistogamous flowers are borne separately and in different positions on the plant. In addition the number of the cleistogamous flowers has been often reduced to a single flower in the leaf axil which seems to be clearly derived from the many-flowered clusters borne terminally on short axillary branches. *Helianthemum glomeratum* is thought to be more advanced than *H. chihuahuense* since the number of chasmogamous flowers is reduced to a usually solitary flower borne at the end of the branches and branchlets. Also chasmogamous flowers are occasionally lacking and the size of the cleistogamous capsule is reduced with only 1-3 seeds in each capsule. When chasmogamous flowers are present in *H. glomeratum*, they are to be found terminating both branches and branchlets while in both *H. rosmarinifolium* and *H. argenteum* the solitary chasmogamous flowers are to be found only at the tips of the major branches. Also in these two species the number of seeds/cleistogamous capsule is never more than one or two. In addition the cleistogamous capsules of both species are more reduced than in any other species. However, *H. argenteum* is considered even more advanced than *H. rosmarinifolium* and also perhaps the most advanced species of the North

American species of *Helianthemum* since (1) the chasmogamous flowers have been reduced to one at the tips of the major branches; (2) the more primitive condition of clustered cleistogamous flowers has been reduced to but one (or rarely two together) in the leaf axils; (3) the cleistogamous capsules are the smallest of all the species studied; and (4) the leaf-size is greatly reduced.

The primitive and advanced features are summarized below:

More than 7000 herbarium specimens were examined of the *Helianthemum* collections of 53 herbaria to whose curators we are most indebted. These herbaria are indicated by their abbreviations following Lanjouw & Stafleu (*Regnum Vegetabile*, ed. 4. 15: 1959.): A, ARIZ, BUS, CHRB, COLO, CU, DS, DUKE, F, FLAS, FSU, GA, GH, IA, ILL, IND, ISC, JEPS, KANU, KY, MICH, MIN, MISSA, MO, MSC, NCSC, NCU, ND, NO, NY, OKL, OKLA, OS, PENN, PH, POM, PUR, RSA, SBBG, SBM, SD, SMU, TENN, TEX, UARK, UC, UMO, US, SCAR (=University of South Carolina), USF, VDB, WIS, WVA.

PRIMITIVE

1. Possession of only chasmogamous flowers.
2. Few but large cleistogamous flowers.
3. Floral parts large.
 - a. Outer sepals of chasmogamous flowers spatulate (and relatively large).
 - b. Outer sepals of cleistogamous flowers large.
 - c. Stigma large.
4. Fruits large and many-seeded.
5. Numerous stamens in the chasmogamous flowers.
6. Carpels 3.
7. Non-hygroscopic testa.

ADVANCED

1. Possession of both chasmogamous and cleistogamous flowers or of cleistogamous flowers only.
2. More numerous but smaller cleistogamous flowers.
3. Floral parts relatively small.
 - a. Outer sepals of chasmogamous flowers linear (and small).
 - b. Outer sepals of cleistogamous flowers much smaller, often reduced to knob-like rudiments.
 - c. Stigma small.
4. Fruits small and few-seeded.
5. Fewer stamens in the chasmogamous flowers.
6. Carpels 2.
7. Hygroscopic testa.

to be continued